Vision of the Honeybee *Apis mellifera* for Patterns with Two Pairs of Equal Orthogonal Bars

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Tests were made of the discrimination by flying bees of black and white patterns that subtend 40° from the point of choice by the bees. The patterns are composed of two pairs of bars at right angles to each other. Bees cannot distinguish the patterns from themselves rotated by 45° or any multiple of 45°. Examples are a cross, a square, a spiral and an irregular pattern of 4 bars in two orthogonal pairs. A chevron pattern can be distinguished from itself rotated by 90 or 180° when the positive pattern is bilaterally symmetrical about a vertical line. Yet these patterns can all be distinguished from each other, so there is no doubt that the bees see them. These results show that the flying bees cannot be using the orientation of edges as cues, nor the spatial arrangement of black areas, or indeed any local feature. It has previously been proposed that, in addition to detectors of orientation and memory of spatial lay-out, bees have global filters for patterns of radial sectors and for concentric circles, which together act as detectors of flower-like shapes, and when these filters are excited the local orientation is ignored. The new observations on patterns of 4 bars are explained by these filters in parallel, except that the peculiar properties of the chevron pattern suggest a further significance for bilateral symmetry. The results imply that vision of these 4-bar targets by flying bees is not assembled from local features, but depends on a few broadly tuned dedicated global filters with large fields for the economical abstraction of a limited range of biologically significant patterns.

Honeybee Insect Vision Memory pattern

INTRODUCTION

Two broad types of mechanisms have been proposed for honeybee visual discriminations of black and white patterns. In the first, the bee compares the image on the retina with a spatial memory of an image seen previously, sometimes called an "eidetic image" after the Greek word for "shape". For example, with reference to large sector targets, one of which is the reverse contrast of the other, "the only factor that can account for the bees' ability to discriminate between these gratings is the exact retinal position of the black and white sectors" (Wehner, 1981, p. 477).

Alternatively, "one part of the pattern discrimination of the honey bee could be reduced to a two-dimensional cross-correlation of the two shapes to be compared" (Cruse, 1972). Quantitative efforts to define this theory measured the fraction of the area or edges in the image that overlap with the other image now in memory, but this method was successful with only a limited range of very large patterns. A bee's memory is unlikely to be large enough to store many pictures to make a correlation in this way, so that some kind of distillation of the information is essential. Early work with bees landing on horizontal targets led to the conclusion that the remembered feature is the degree of disruption of the image (von Frisch, 1915; Hertz, 1929, 1933), which at that time explained the confusion by the bee of some images that look very different to us. This idea persisted into recent times—for example, Cruse (1972) continues "Another part of the pattern discrimination could be a comparison of the number of alternating stimuli in the ommatidial elements produced by the movement of the shapes relative to the flying bee." In this early work, however, the bees were obliged to rely on non-spatial properties of the patterns because when landing on a flat table they had no reference direction for information about the distribution of black areas in the image, spatial frequency in relation to range, or the orientation of edges.

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Thirty years ago it was discovered that the orientation of a contour can be discriminated by hovering (fixating) bees if the pattern is on a vertical surface (Wehner and Lindauer, 1966). At the time it was thought that "the patterns are projected to a central nervous grid, which preserves the intensity distributions spatially according to a fixed coordinate system" and therefore it was concluded that "the contrast-invariant information about the direction of the stripe corresponds to a further step in data processing" (Wehner, 1972). During this work with fixating bees and very large targets, it was discovered that the memory appears to be fixed in the region of the eye where it was first processed, a finding that further strengthened the idea that the bee can remember an "eidetic image" of a previously seen image. With patterns of regular sectors subtending 130° at the choice point the bees could discriminate between 16 and 32 sectors and could distinguish the rotation of 8 black sectors by an angle of 22.5° (review, Wehner, 1981). Some of these results were evidence for orientation filters, others for local cues or memory of the spatial lay-out, and the discrimination of a large sector pattern from itself with reversed contrast did not necessarily demonstrate that the bees laid down the whole image in memory. In fact, the two features, lay-out and orientation, were not separated in the analysis. There is now evidence that bees rely mainly on the margins of the target for the lay-out of areas of black (Horridge, 1994).

One objection to the idea of a memorized image for all situations is that bees confuse many patterns that look quite different to us. A more significant objection is that bees abstract the generalized feature of average orientation if they are tested with quite different patterns (Lindauer, 1969) or if they are trained using gratings with randomized spacing (van Hateren et al., 1990). Also, when trained with circles and sectors of randomized spacing they discriminate a variety of circular and radial patterns (Horridge and Zhang, 1995). Theories that rely entirely on each new image being superimposed upon the memorized image are also ruled out by motion of the target, by differences in range or scale, in orientation, and by the observations of confusion between mirror-images and between shapes that are different. Another objection to a memorized image for later consultation is the large amount of information that image storage requires.

In the second type of theory the bee abstracts a few simple cues from the image and puts only these cues into memory. As summarized by Lindauer (1969), "after a drastic filtering process, those key figures, which are essential for the survival of the species, are selected from the optical diversity of the environment." In this model of the visual system, there is a limited selection of dedicated filters which respond to particular aspects of the image and these responses are stored or compared with previous responses of the same filters. This is more economical than storing the whole image but throws away the detailed origins of the inputs. A well-known example is the use of three dedicated filters in colour vision, giving rise to the discrimination of many colours but failure to analyse them into wavelengths.

There is now strong evidence that bees have such filters for spatial vision and store their outputs non-spatially. The disruption of the pattern, irrespective of shape, in modern terms, is an abstracted feature of a pattern that is the response of a temporal filter. More recent examples are the orientation detectors which have been inferred from experimental discriminations of differently oriented black and white edges irrespective of the pattern (Wehner, 1971; van Hateren et al., 1990). Orientation filters, as reviewed by Srinivasan (1994), however, will not account for many discriminations such as those presented here, where there is no difference in average orientation.

One way to improve our model would be to demonstrate that the honeybee's performance is explained by a small number of filters in each region of the eye, beyond which the image is not discriminated. In turn, this objective implies that we should study examples of bee vision where discrimination fails although the bees obviously see two relatively simple targets which are different. The first step in this direction was the experimental demonstration that bees cannot discriminate a St George's cross (+) from a St Andrew's cross (×). From this result it was concluded that edge orientations sum as vectors within quite large regions of the target and therefore cancel when they are orthogonal because the orientation filters have large spatial fields and angular turning curves 90° wide at the 50% sensitivity level (Srinivasan et al., 1994). This model predicts, however, that patterns with pairs of equal bars at right angles are all indistinguishable from each other irrespective of how a constant number of bars are distributed over the target. This prediction is clearly contradicted by the results to be presented. A direct test of the size of the regions of the target over which orientations are summed found them to be the size of quadrants that subtend 15–20° from the choice point (Zhang and Horridge, 1992).

The results to be presented rule out the use of any orientation filters and also the eidetic image or spatial lay-out of areas of black because discrimination fails, so we have to look for an entirely different set of filters to explain the successes. Patterns of sectors and concentric circles of similar disruption can be discriminated even on a horizontal surface (Hertz, 1933). We have now found that bees innately prefer radial patterns and avoid circular patterns displayed on a vertical surface (Lehrer et al., 1995), showing that some kind of intrinsic detectors are present. When one target is selected randomly from a variety of sector patterns during the training, and the other target randomly from concentric circles, flying bees learn to generalize any sector-like pattern from any circle-like pattern, and both of these separately from a chequered pattern (Horridge and Zhang, 1995). This result strengthens the proposal of additional global filters that do not sum orientation over the whole target. On the basis of all these observations, it has been proposed

(Horridge, 1994) that bees have innate filters for radial and circular patterns that correspond to the Lie transforms (Dodwell, 1983). In this model, flying bees use a combination of dedicated global filters in regions subtending 40° at the front of the eye. The peculiar properties of patterns with two pairs of bars at right angles provide further evidence for this model.

MATERIALS AND METHODS

In every experiment a group of worker honeybees from a local hive were each distinctly marked with a combination of coloured spots and trained to make a choice between two targets placed on the back walls of the compartments in the Y-choice apparatus (Fig. 1), which has now generated many studies following a standard paradigm. The walls of this apparatus are of white card, the roof is of transparent Perspex. The flying bees are able to see both patterns when they enter the choice chamber. Both targets have a hole 2 cm in diameter at the centre but only one, called the positive target, gives access to a reward of sugar solution in water in a clean feeder within a box behind the target. The concentration of sugar is just sufficient to bring back the marked bees for more without attracting recruits, and therefore depends on the weather and on alternative supplies available to the bees. The other target, called the negative one, provides no reward, only a blind tube. The targets are interchanged every ten minutes so that the bees cannot learn the location of the reward. Instead they have to obtain visual cues from the target at a range greater than 27 cm. The flying bees do not hover or fixate the patterns as they fly in, but they either veer to one side in flight or they scan first one target and then the other from the choice chamber. During training, the bees obtain a reward at every correct choice.
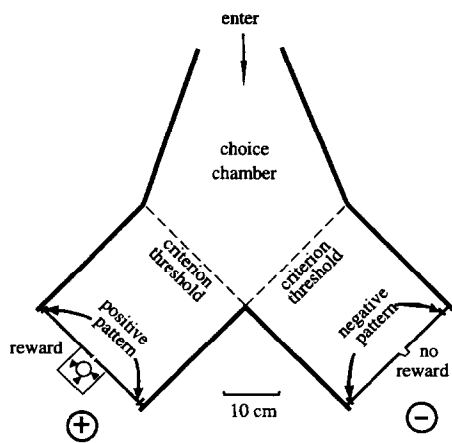

FIGURE 1. Top view of the Y-maze apparatus. The sides are opaque, the top is transparent. The flying bees enter through the wide aperture to the choice chamber from which they can see both of the targets at the same time. They choose one of two chambers bearing a target presented in the vertical plane on the back wall. Behind the positive target is a reward box containing sugar solution which is accessible through the hole at the centre of the target. The criterion for scoring the performance is when the flying bee first crosses the dashed line.

Each experiment involved training a group of 8–12 marked bees to enter the apparatus for a reward. This number of bees was used because the weather was cool and dull, but fewer bees and a weaker sugar solution are needed on hot days. Outside temperatures ranged from 18–25°C. In most of the experiments, here called "train and test", the training and recording of every choice was continuous, with the targets interchanged and the reward moved to the other side every 10 min. At first the naive bees return to the side where they were last rewarded, then after a few changes they go at random to one target or the other, but with some targets they eventually veer to the correct side (on average over several visits) showing that they have learned to look at the targets as they enter the apparatus. Each choice of each individual bee is separately recorded in each 10 min period between changes. The criterion of a correct choice is decided when the flying bee first crosses one of the lines (dashed in Fig. 1) which define the two arms of the Y-choice chamber. Bees that make an error almost always inspect the negative target closely and then go back to the positive target, but only their first choice is recorded. As a precaution against unwanted cues, such as odour, or differences in the central tube or in the surround of the pattern, in some of the following experiments, the patterns were interchanged by rotating them both by the appropriate angle, so the bees saw the same pattern but in a different orientation and the reward was moved to the other side. It should be noted that many experiments have the important result that the bees cannot discriminate the two targets, so any possible "unknown cues" were clearly of no help. If the bees are able to learn the discrimination, the proportion of correct choices in each 10 min period reaches an asymptote after $1\frac{1}{2}$–2 h. The counts of choices for the results therefore begin after $1\frac{1}{2}$–2 h of training, and run for 8–12 periods of 10 min each, i.e. for a further period of $1\frac{1}{2}$–2 h. This means that one or two experiments can be done in a day.

Each bee visits once or twice, rarely 3 times, in each period of 10 min. The proportion of correct choices, and the total number of choices are counted in each 10 min period. If the bees cannot discriminate the targets, the performance will be 50% correct. The fraction of correct choices for each of the 8–12 periods of 10 min is calculated and the means and SD of these fractions are tested by the χ^2 test for a difference from 0.5 and converted to percentages. Further details are given in van Hateren et al. (1990).

Because the theory proposes filters in parallel, any one of which is sufficient for a discrimination, the patterns must be selected with care. Each pattern contains the same amount of edge and the same area. In fact, all the patterns consisted of the same four equal bars, which avoids differences in luminance or total amount of black in a pattern, because the bees may use these cues if all other aspects of the pattern are similar. Bees can use the average orientation in the whole target if it is not zero (Srinivasan et al., 1994), so there is little point in using anything but pairs of bars at right angles. A sufficient var-

iety of patterns can be made with 2 pairs of orthogonal bars and more bars are not necessary. The intention is to study the effect of spatial lay-out of the bars irrespective of other factors. In many of the experiments reported here, the two patterns were identical except that one was rotated relative to the other when the reward was moved to the other side, so that many possible unwanted cues are avoided.

The targets were generated by computer and printed on discs 25 cm in diameter on standard white copying paper, and all patterns were photocopies of an original from the same machine with the same settings. The 4 black bars of constant size $(8.5 \times 2.0$ cm), are arranged in different ways but always in two pairs at right angles: the results themselves show that the bars can be seen by the bees.

Previous work has shown that flying bees can resolve the gratings and bars used here. The resolution of the bee's eye for the equal black and white stripes of a grating is equal for vertical and horizontal gratings, and is adequate to give 65% correct choice at a period of 4°, which falls to 50% at a period of 3°, measured with the same Y-choice apparatus (Srinivasan and Lehrer, 1988). Single bars are more easily resolved than gratings, and our bars 2 cm wide are similar to those in a grating of period 8.9°. Each pair of patterns is illustrated with the percentage choice and the statistical significance of the difference from 50% (random choice).

RESULTS

Failure to detect rotation

As long as the 4 bars are in orthogonal pairs, many arrangements of them subtending 40° at the choice point are indistinguishable by flying bees from themselves rotated by 45° (Fig. 2). The case of the two crosses [Fig. 2(a)] was reported by Srinivasan et al. (1994), the two squares [Fig. 2(b)], and the two irregular figures [Fig. 2(e) rotated by 180°] by Horridge and Zhang (1995). The spiral pattern [Fig. 2(c)], which is new, is not discriminated from itself rotated or from its own mirror image [Fig. 2(d)]. These results show that neither orientation of edges nor spatial lay-out of black areas is used as a cue. The processing of the image is therefore not achieved by assembly from local features. All these patterns would excite a global filter for radial sectors or that for concentric circles, or both to some extent, and therefore the results fit the proposals that the radial filters act irrespective of rotation and that excitation of the radially symmetrical filters blocks orientation detectors. Some new data will demonstrate the negligible part played by orientation detectors when the patterns are radially symmetrical crosses.

Discrimination of 45° by flying bees [Fig. 3(a)]

The single stripe is composed of two of the standard black bars, as used for the other experiments. One stripe is vertical, the other inclined at 45°. The one inclined at
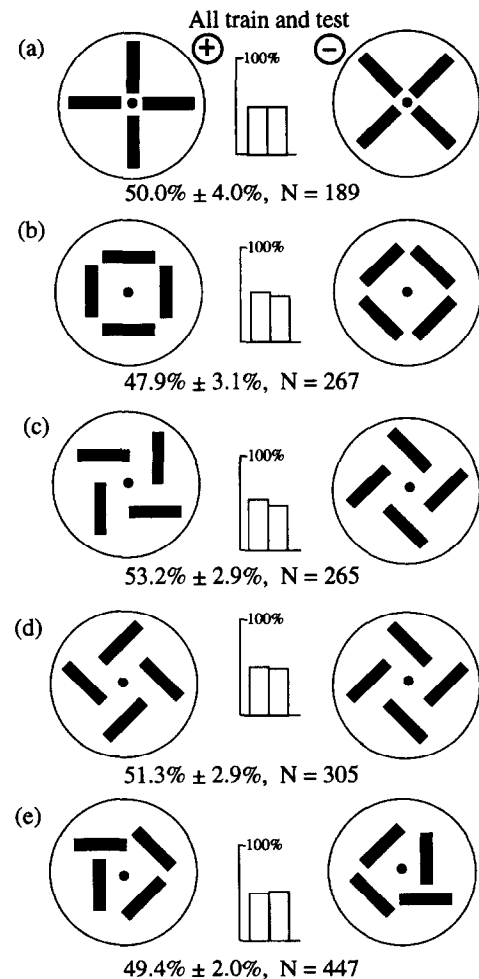

FIGURE 2. These patterns of two pairs of orthogonal bars cannot be discriminated from themselves rotated by 45° by flying bees when they subtend 40° at the choice point. (a) The cross. (b) The square. (c) The spiral. In (d) the spiral cannot be discriminated from its mirror image, and in (e) the irregular pattern is tested against itself rotated through 180°.

45° was selected as the positive target because it is already known that many insects have a preference for vertical edges, so the training was aimed against any such possible tendency. The result, in agreement with previous work (Srinivasan, 1994), was $58.0 \pm 2.3\%$ correct for $n = 390$; $P < 0.005$. The difference of 45° in angle can be learned but the performance is poor in comparison with that of bees fixating on single stripes that subtend 130° by more than 5° at the choice point (Wehner, 1968).

Failure to see orientation components in the crossed bars [Figs 2(a), 3(b–d)]

With a new group of bees, the cross was again tested against itself rotated by 45° [Fig. 2(a)]. The result $(54.3 \pm 3.8\%, n = 272)$, not illustrated in Fig. 3, was similar to that previously published (Srinivasan et al., 1994; Horridge and Zhang, 1995). Flying bees cannot learn this discrimination task when the target subtends 40° at the eye, although the training is continued for several hours and the pattern contains more orientation than the two bars in Fig. 3(a).
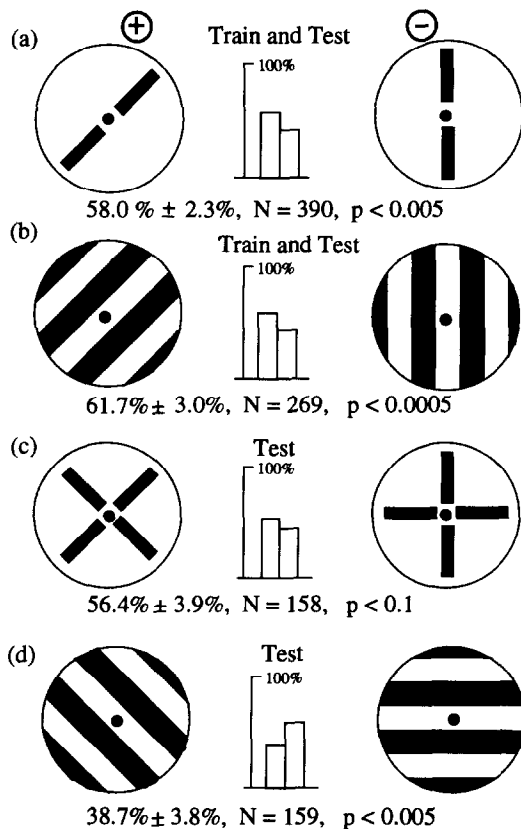
FIGURE 3. (a) Two bars in a straight line can be discriminated from themselves rotated by 45°. (b) A grating is well discriminated from itself rotated by 45°. (c) The bees trained with (b) are now tested with the two cross patterns, but their performance is hardly improved by their previous experience. (d) When the same bees, trained with (b), are tested with both gratings rotated by 90°, they prefer the pattern that most resembles the previous positive pattern. They use the orientation cue in (d) but not that in (c).

The next day the same group of bees was trained to discriminate a regular grating from itself rotated by 45°, again with the vertical edges negative [Fig. 3(b)]. The grating period was 12°. As might be expected from the bold pattern, the performance is better than with the single stripe. The result was $61.7 \pm 3.0\%$ correct, $n = 269$, $P < 0.0005$. The performance was not as good as previously found with regular gratings in this apparatus (Srinivasan, 1994; Zhang and Srinivasan, 1994a) because the vertical stripes were in the negative pattern and the training period was short.

The same group of bees that had failed with the crossed bars and were now trained with the gratings in Fig. 3(b) were tested at intervals of 20 min with the two crosses in Fig. 3(c) while their training on the gratings continued. The tests with the crosses were conducted with a reward for both targets for 5 min at a time, and the two sides were interchanged at alternate tests. The result, $56.4 \pm 3.9\%$, $n = 158$, $P < 0.1$, is disappointing [Fig. 3(c)]. Although the training with the two gratings at 45° is continued between the tests, they still fail to see that one cross of 4 bars is rotated by 45° relative to the other. Although training towards orientation on a con-

tinuum can have an influence in other examples (Wehner, 1971; Zhang and Srinivasan, 1994b), it is ineffective in this case. Even when the previous experience is definite and strong, as in this example, the bees still act as if they cannot use the orientations within the radial pattern.

The bees trained to discriminate two gratings at 45°, were also used for an additional experiment. During the training in Fig. 3(b), the bees were given forced-choice tests with the same pair of gratings, but rotated by 90°. Both patterns were rewarded during each 5 minute period of the tests, and the two sides were interchanged at alternate tests. Both of the grating patterns in the tests are at right angles to their former positions [Fig. 3(d)]. The bees now prefer the horizontal grating, not the mirror image of the target that was formerly the positive one. The result is $38.7 \pm 3.8\%$, $n = 159$, $P < 0.005$. The bees select the target which is more similar to the positive target that they have learned. The mirror image of the positive target is not confused with the positive target. This result is readily explained if some of the orientation filters have broad tuning curves in the angular domain, as suggested by Srinivasan et al. (1994). The point here, however, is that the trained bees can use the not-so-obvious orientation cue in Fig. 3(d) but not that in 3(c).

So far we know of several patterns composed of 4 bars that bees cannot discriminate from themselves rotated by 45°—the cross, the square, the spiral and the irregular pattern (Fig. 2). There must certainly be many more that are intermediate patterns between these examples.

A pattern with bilateral but not radial symmetry

The same four bars can be rearranged in a chevron pattern with strong bilateral symmetry (Fig. 4) that looks different to us when rotated by any angle. This pattern has two of the bars of the cross in Fig. 2(a) and two of the bars of the square in Fig. 2(b) but lacks radial symmetry. In fact, two of the bars are orthogonal to the radii and two are orthogonal to a pattern of circles, so it could be said to have cancelled the orientation for the orientation detectors and also to have no radial or circular symmetry for the detectors of flower-like shapes.

This pattern can be discriminated from itself inverted in the situation in Fig. 4(a) with a performance of about 80%. The result was $79.7 \pm 2.5\%$, $n = 253$, which is in the range that one finds with flying bees with a discrimination of gratings at 90° or radial targets vs circular targets (Horridge and Zhang, 1995). When one of the chevrons is not upright, however, the performance drops drastically to $61.5 \pm 3.3\%$, $n = 218$, $P < 0.001$ [Fig. 4(b)]. With a different group of bees in experiments separated by 3 months, and the positive and negative targets reversed [Fig. 4(c)], the result was $62.3 \pm 2.0\%$ correct and still significant [see also Fig. 5(d)]. However, on the next day, the same group of bees could not discriminate the positive chevron pattern lying on its side from itself rotated by 90° as in Fig. 4(d). A different group of bees could not discriminate the mirror images in Fig. 4(e)
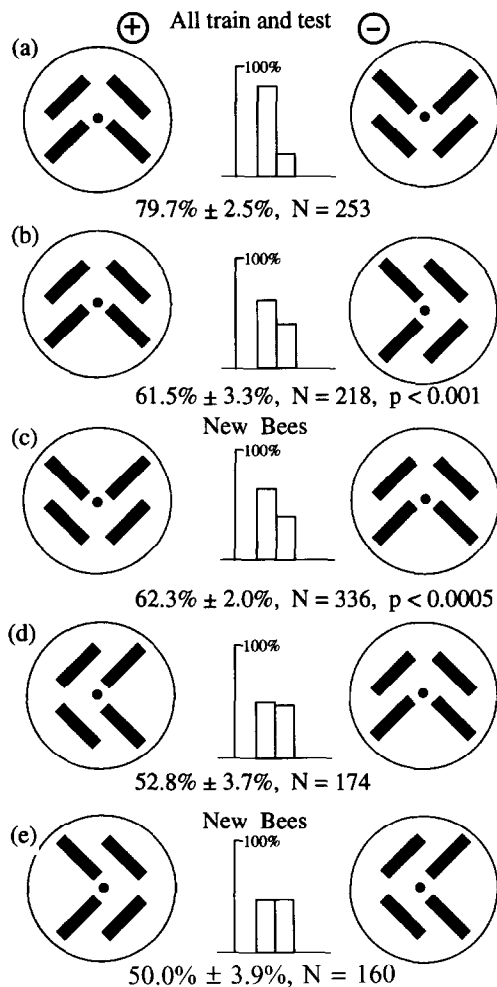
FIGURE 4. Bilateral symmetry assists discrimination. The positive chevron pattern of 4 bars is discriminated from itself rotated by 90° or 180° when it is symmetrical about a vertical line. In the other combinations without the symmetry the bees did not discriminate.
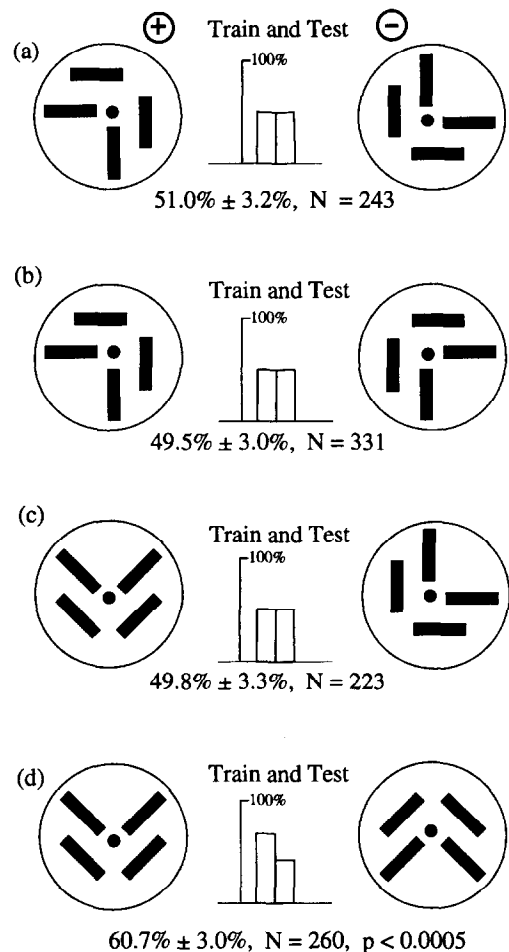

FIGURE 5. Chevron patterns are not discriminated when they both lack a vertical axis of symmetry. The result in (c) shows that the detection of bilateral symmetry about the vertical is too broadly tuned to detect a rotation by 45°. In (d) the same bees show that they see the pattern.

although in each corresponding quadrant of the targets the bar has been turned through a right angle.

These results suggested that there is something special about the chevron pattern when it is upright or upside down, or that there is something special about bilateral symmetry, as indeed there is in our own vision. The next step with a new group of bees was to train with the chevron patterns rotated so that two of the bars are horizontal and two are vertical. This operation spoils the discrimination of rotation, either by 180° or by 90°. The bees do not notice the direction that the chevrons point [Fig. 5(a)], nor do they distinguish between mirror images [Fig. 5(b)]. Surprisingly, the downwardly pointing chevron, with the plane of symmetry vertical, was not discriminated at all from itself rotated by 45° [Fig. 5(c)], but the upwardly pointing chevron was discriminated, although not particularly well, from itself rotated by 90° [Fig. 4(b)]. The performances in Figs 4 and 5, and particularly in 5(c), taken together, show that if there is a global filter for this pattern, it has broad angular tuning and is symmetrical about a vertical line.

The experiments illustrated in Figs 5(a)–(c) were done

during a week of observations upon one group of individually marked bees, in a fruitless effort to train them with a different pair of patterns each day. There were two or three losses of marked bees which were replaced by new recruits each day in a group of 8–12 bees. The bees learnt none of these combinations, so finally [Fig. 5(d)], the same bees were trained and tested on the inverted and normal chevrons, with a performance of 60.7 ± 3%, $n = 260$, $P < 0.0005$. This is the same result as before [Fig. 4(c)]. They certainly see the chevron pattern, as shown by the fact that they discriminate its rotation by 90 or 180° when the positive target is symmetrical about a vertical line.

The pattern types are discriminated from each other

There is no doubt that all the patterns are visible to the bees because the different types are discriminated from each other (Figs 6 and 7). Only a few of the hundreds of possible combinations have been tested but the main types of pattern are clearly distinct to the bees. Rotation of the patterns does not seem to influence this result. Some of the combinations are worth special com-
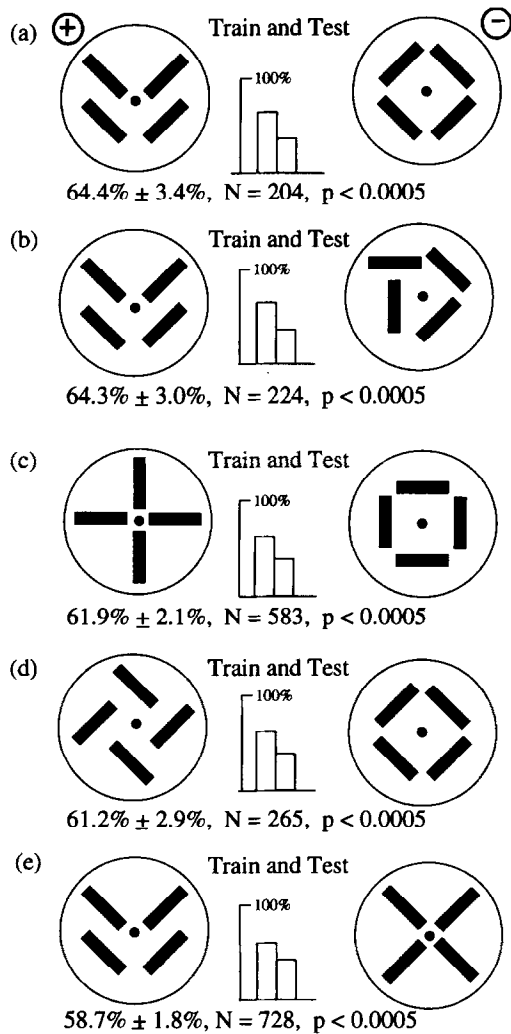
FIGURE 6. The different types of pattern are discriminated from each other. Together with Fig. 7, these results are in order of decreasing performance.
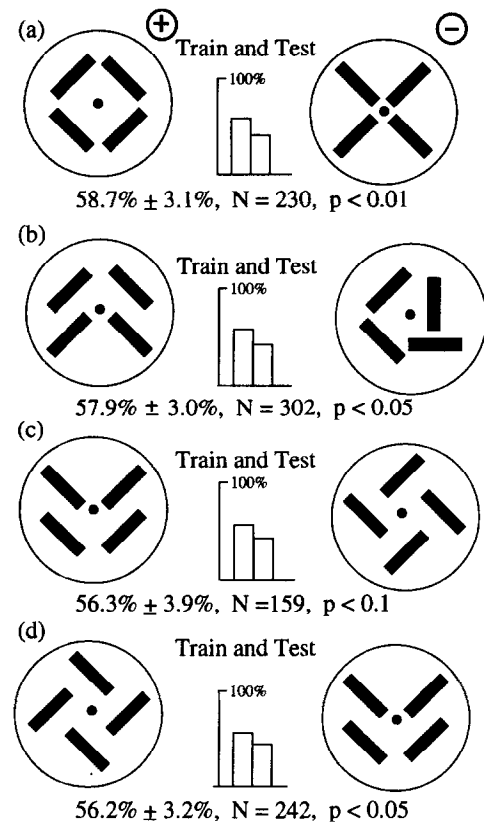

FIGURE 7. More patterns, in order of decreasing performance, that are discriminated from each other. Some of these patterns would excite more than one of the proposed filters for sectors, circles and bilateral symmetry. Any quantitative model of filters in bee vision must fit this data.

ment. Although the chevron pattern contains two of the bars of the cross and two of the square, it is discriminated well from either of them [Figs 6(a,e)]. The irregular pattern in Fig. 2(e) cannot be discriminated from itself rotated by any angle. Possibly this figure excites a filter for flower-like shapes, or possibly four separate orientations are too much for the memory of the bee. However the inverted chevron pattern is readily discriminated from this irregular pattern [Fig. 6(b)] with a performance of 64.3 ± 3%, n = 224, P < 0.0005. Again, there is something special about the chevron [Figs 4(a) and 6(a,b,e)] in that bilateral symmetry about a vertical line assists discriminations.

DISCUSSION

The proposal that guides these experiments is that the flying bee has a few broadly tuned innate filters for global patterns of biological significance. Flying bees can discriminate the difference of 45° in the orientation of two bars in a line [Fig. 3(a)], but average orientation was excluded as a cue by working with pairs of bars at right

angles. None of the combinations of four bars can be discriminated from itself rotated by 45°, although they contain more information about orientation than the single bar. The results in Figs 2–5 cannot be explained by the orientation of individual bars nor by a mechanism that compares the distribution of black areas, and there are no other local features. Therefore there must exist subtle global filters. Only one of the 4-bar patterns tried can be discriminated from itself when rotated, and that is the chevron [Fig. 4(a)]. In most combinations, however, the patterns can all be discriminated from each other (Figs 6 and 7), especially if they obviously differ in the amount of radial or circular contour.

A separate series of experiments recently found that bees have an innate preference for radial patterns, and that they distinguish between them and circular patterns without learning (Lehrer et al., 1995). Therefore they have some kind of detectors for these patterns. Another previous work, closely related to the present study, found that bees discriminate very well between black and white patterns of randomized radial sectors vs patterns of randomized concentric circles, with as high a percentage of correct choices as with regular black and white gratings (Horridge and Zhang, 1995). We also know that for flying bees the global average orientation is of higher priority than the local orientation (Zhang et al., 1992). These results led to the proposal that bees have a set of

innate global filters for radial patterns and another set for patterns like circles, as a rapid way of separating flower shapes from random background and for identifying different flower shapes, in parallel with orientation detectors and colour (Horridge, 1994). This model, with radial and circular filters similar to the Lie series of co-ordinates (Dodwell, 1983), implies that the detectors of flower-like shapes must block the discrimination of orientation and perhaps other features, in a winner-take-all strategy.

The proposal of innate global filters in bee vision suggests numerous experiments. In the course of the work with patterns of 4 bars the special properties of the chevron pattern were discovered. This 4 bar pattern has no net orientation and no radial or circular symmetry, but it has a strong bilateral symmetry. When looking for new filters in the visual system there is little point in working with patterns which carry cues that would excite the known filters. The result with the chevron suggests that bees have a filter beyond those for circles or radial patterns, or for average orientation, and that it is related to bilateral symmetry, which is already known to have a broad biological significance for bumblebees (Møller, 1995).

A small number of innate global filters can provide an economical mechanism for the commonly encountered patterns in any dedicated visual system (or, indeed, any other system) with a limited repertoire. To detect significant patterns in a variety of situations, such filters need to be broadly tuned so as not to reject likely targets, but broad tuning makes them less selective in some respects. The system is made both generalized and specific by combining the outputs of several filters. For example, there are only three types of broadly overlapping colour filters in man and in the bee, and they are relatively insensitive to motion, shape or other features. Similarly, orientation filters in man and bee are broadly tuned in angular orientation and insensitive to motion. In insect motion perception, the slow filters peak broadly below 10 Hz while the fast filters peak above 10 Hz (Horridge and Marcelja, 1992). As illustrated by the example of colour vision, a system based on the relative responses of filters in parallel can make numerous discriminations with few pathways and is far more efficient than a system that must put the whole image into memory for a later consultation in which an unpredictable combination of features would be required. However, in addition to the filter responses, beyond which the spatial memory of inputs is lost, bees also make use of contrasts separated by large angles projected on the retina, as in their vision of landmarks.

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